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SYSTEMATICS AND DISTRIBUTION OF
CERATIOID ANGLERFISHES OF THE GENUS
LOPHODOLOS (FAMILY ONEIRODIDAE)

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ABSTRACT. The genus *Lophodolos* of the family Oneirodidae is reviewed on the basis of all known material. Two species are recognized, *L. acanthognathus* Regan and *L. indicus* Lloyd. *Lophodolos dinema* Regan and Trewavas is considered a junior synonym of *L. indicus* Lloyd. The tentative distribution of each species is plotted and a key to the species of the genus is provided.

INTRODUCTION

The genus *Lophodolos* was erected by Lloyd (1909a) to include a single species, *L. indicus*, on the basis of a specimen collected from the Indian Ocean by the Royal Indian Museum Survey Ship INVESTIGATOR. Since that time three additional species have been described: *L. acanthognathus* Regan (1925), to which have been referred more than 60 specimens from the Atlantic and western Pacific oceans; *L. lyra* Beebe (1932), synonymized with *L. acanthognathus* by Regan and Trewavas (1932); and *L. dinema* Regan and Trewavas (1932), represented by a single specimen from the South China Sea.

The number of female specimens of *Lophodolos* has doubled since the appearance of Bertelsen's (1951) monograph on the Ceratioidei. In spite of extensive information gained from this increase in material, taxonomic study of the genus is by no means complete. Metamorphosed males are unknown; thus, species are based only on females. The separation of species is based on only a few characters, the most important being the morphology of the esca and the length of the illicium. Differences in

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these two characters merge in specimens less than 25 mm standard length, making differentiation particularly difficult. Nevertheless, the material presently known appears to represent only two forms: *L. acanthognathus* Regan (1925) and *L. indicus* Lloyd (1909a).

METHODS AND MATERIALS

Standard lengths (SL) were used throughout. Measurements were taken on the left side of the fish whenever possible and rounded to the nearest 0.5 mm in specimens greater than 20 mm, and to the nearest 0.1 mm in specimens less than 20 mm. To insure accurate fin-ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the dorsal surface of the esca bulb, excluding esca appendages. Terminology used in describing the various parts of the angling apparatus follows that of Bradbury (1967). Definitions of terms used for the different stages of development follow those of Bertelsen (1951: 10–11).

Locality data is given for primary type material only. Complete locality data for all specimens examined may be obtained by writing to the author.

The generic diagnosis (much of which is taken from osteological evidence presented elsewhere: Pietsch, 1974) and description are based on 98 metamorphosed females ranging from 6.0 to 77.0 mm (metamorphosed males are unknown). Larvae were described by Bertelsen (1951: 106). Study material is deposited in the following institutions:

BMNH	British Museum (Natural History), London.
BOC	Bingham Oceanographic Collections, Peabody Museum of Natural History, Yale University.
BZM	University of Bergen Zoological Museum.
CAS	California Academy of Sciences, San Francisco.
FMNH	Field Museum of Natural History, Chicago.
GNM	Natural History Museum of Göteborg.
IMC	Indian Museum, Calcutta.
ISH	Institut für Seefischerei.
LACM	Los Angeles County Museum of Natural History.
MCZ	Museum of Comparative Zoology, Harvard University.
NIO	National Institute of Oceanography, Surrey, England.
NYZS	New York Zoological Society.

ROM	Royal Ontario Museum.
SIO	Scripps Institution of Oceanography, La Jolla.
SU	Stanford University (collections now housed at the California Academy of Sciences, San Francisco).
UMML	University of Miami Marine Laboratory.
USNM	United States National Museum, Washington.
ZMUC	Zoological Museum, University of Copenhagen.

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I thank Erik Bertelsen and Karel F. Liem for critically reading the manuscript and offering valuable suggestions. Thanks are also due the following persons and their institutions for making material available: Robert J. Lavenberg and Jerry Neumann (LACM); Erik Bertelsen and Jørgen Nielsen (ZMUC); Gerhard Krefft (ISH); Richard H. Rosenblatt (SIO); W. B. Scott (ROM); William N. Eschmeyer and Tomio Iwamoto (CAS); Alwyne Wheeler (BMNH); C. Richard Robins (UMML); Nigel Merrett and Julian Badcock (NIO); Robert H. Gibbs, Jr. (USNM); Robert K. Johnson (FMNH); Thomas A. Clarke, Hawaii Institute of Marine Science, University of Hawaii; and Michel Legand, Office de la Recherche Scientifique et Technique Outre-Mer, Nouméa, New Caledonia. A. G. K. Menon of the Zoological Survey of India, Calcutta, kindly provided information and a sketch of the esca of the holotype of *Lophodolos indicus*. Finally, I thank Patricia Chaudhuri for the fine illustrations.

SYSTEMATICS

Genus *Lophodolos* Lloyd, 1909a

Lophodolos Lloyd, 1909a: 167 (type species *Lophodolos indicus* Lloyd, 1909a, by original designation and monotypy). Fowler, 1936: 1337, 1339–1340, 1365, fig. 560 (brief description after Regan, 1926; in key). Pietsch, 1974: in press (osteology; relationships).

Lophodolus (emended or erroneous spelling of *Lophodolos* by various authors).

Oneiroides Murray and Hjort, 1912: 104, fig. 90 (in part; erroneous designation; type species *Oneiroides eschrichtii* Lütken, 1871, by original designation and monotypy).

Lophodulus (erroneous spelling of *Lophodolos* by various authors).

Diagnosis. The genus *Lophodolos* is distinguished from all other genera of the family Oneirodidae by the following characters: dorsal profile of frontal bones concave; ventromedial exten-

sions of frontals absent; posterior end of frontal in contact with respective prootic; pterosphenoid absent; pterygiophore of illicium emerging between or behind sphenotic spines; symphysial and sphenotic spines extremely well developed; medial ends of hypobranchials II (as well as hypobranchials III) approaching each other on the midline (see Pietsch, 1974: in press).

In addition, *Lophodolos* is unique in having the following combination of characters: snout short, mouth large, cleft extending past eye; vomerine teeth absent; anterior end of pterygiophore of illicium exposed, its posterior end concealed under skin; articular spines present, quadrate spine larger than mandibular spine; angular spine present; pharyngobranchials I and II absent; pectoral lobe short and broad, shorter than longest rays of pectoral fin; operculum bifurcate; suboperculum slender throughout length, its upper end tapering to a point, its lower end rounded, with a small anterior projection in some adolescent specimens; skin naked, covering caudal fin to some distance from fin base.

Description. Body relatively long, slender, not globular; jaws equal anteriorly; lower jaw with an unusually long symphysial spine; oral valves well developed, lining inside of both upper and lower jaws; two nostrils on each side at end of a single short tube; labial cartilage well developed (Pietsch, 1972a: 31); angular bone terminating as a well-developed spine; eye subcutaneous, appearing through a circular, translucent area of integument; gill opening oval in shape, situated just postero-ventrad to pectoral lobe; skin naked (embedded dermal spines cannot be detected microscopically in cleared and stained specimens); lateral line papillae as described for other oneirodids (Pietsch, 1969, 1972b); ovaries paired; pyloric caeca absent.

Illicium length 11.1 to 138.0 percent of SL, becoming longer proportionately with growth (Fig. 1); anterior end of pterygiophore of illicium exposed, emerging on head between or behind sphenotic spines, its posterior end concealed under skin; esca with a pair of unpigmented, bilaterally placed appendages arising from distal surface.

Teeth slender, straight, all depressible, and weakly set (easily damaged or lost), in overlapping sets as described for other oneirodids (Pietsch, 1972b: 5, fig. 2); teeth in lower jaw larger and more numerous than those in upper jaw; number of teeth in lower jaw 200 to 280 (based on five specimens, 57.0–77.0 mm); pharyngobranchial II absent; pharyngobranchial III well developed and bearing numerous teeth.

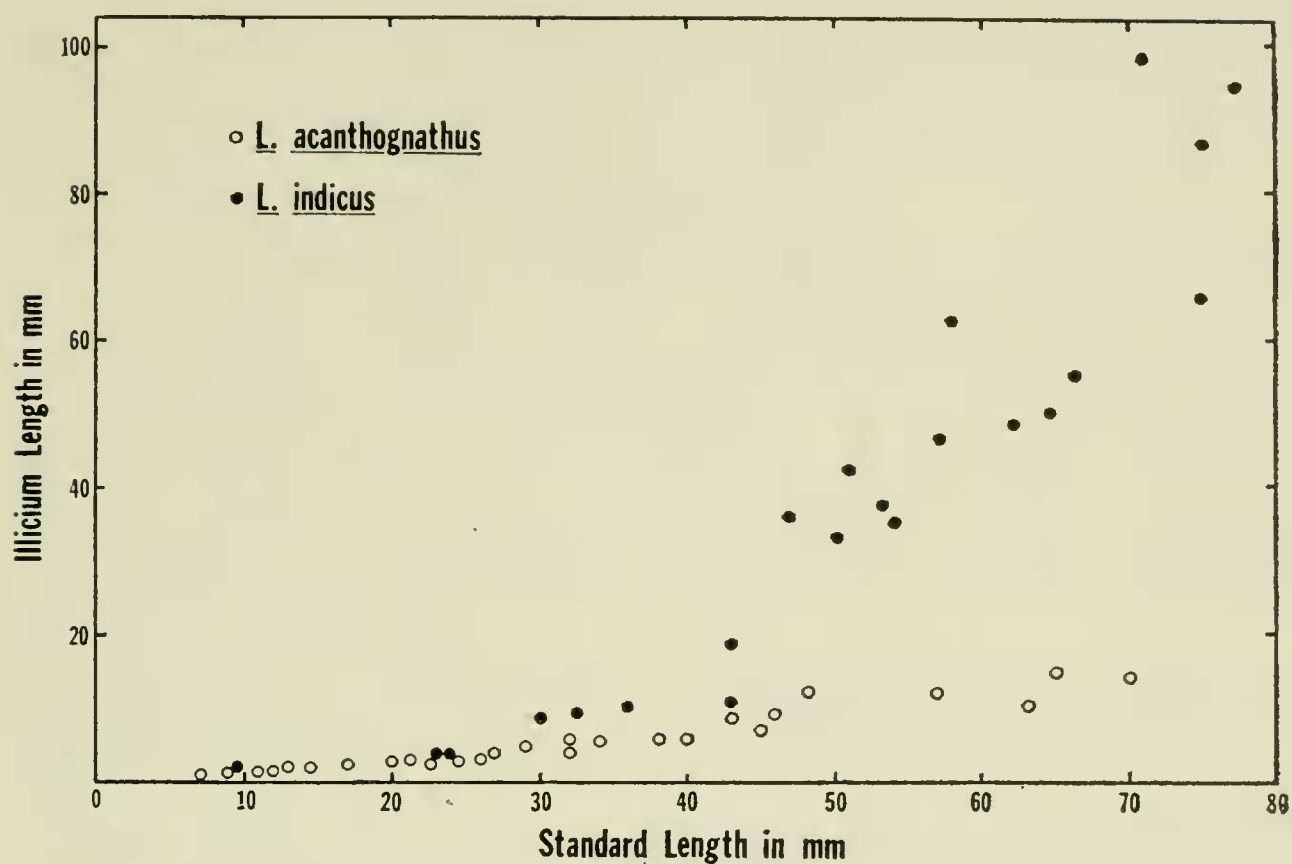


Figure 1. Relationship of illicial length and standard length for species of *Lophodolos*.

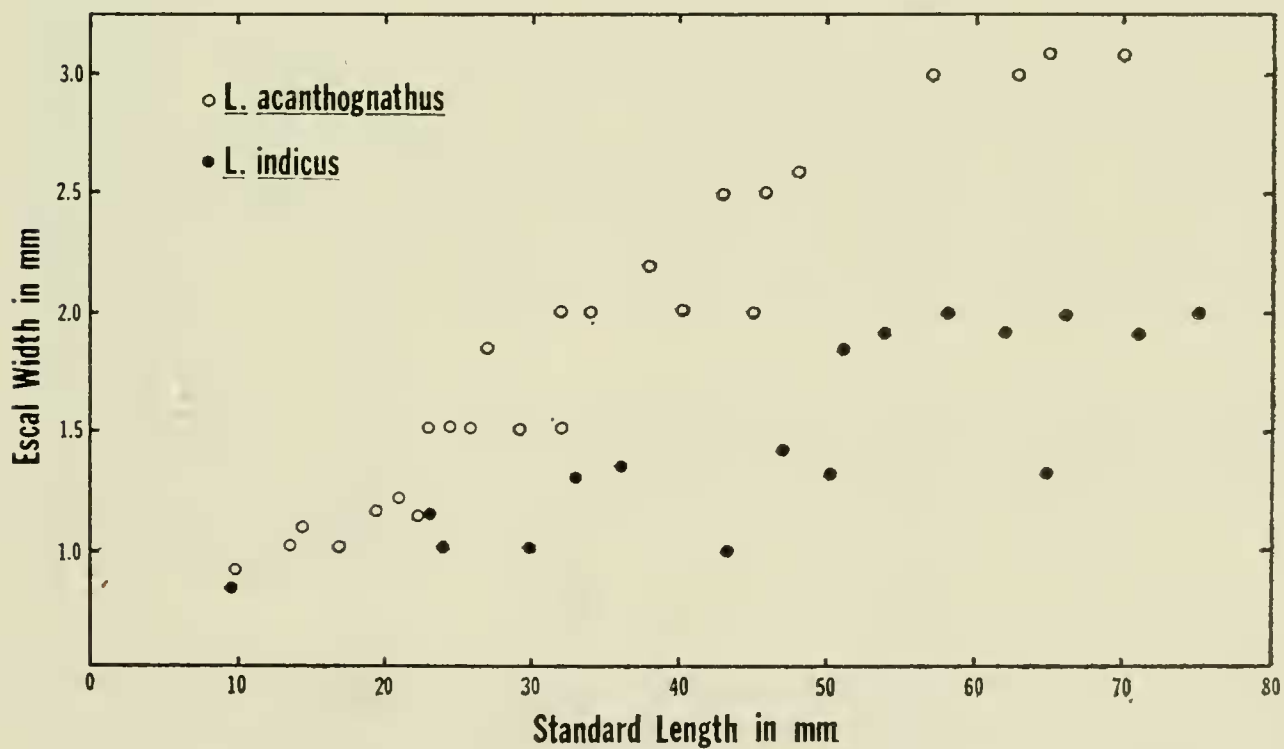


Figure 2. Relationship of escal bulb width and standard length for species of *Lophodolos*.

Table 1. Fin-ray frequencies for larvae and species of *Lophodolos*.

	Dorsal				Anal			Pectoral (left side)					
	5	6	7	8	4	5	6	7	17	18	19	20	21
<i>Lophodolos</i> sp. larvae ¹	1	4			2	3			1	2	1	1	
<i>Lophodolos acanthognathus</i>	5	17	1		2	20	1		3	8	5	3	
<i>Lophodolos indicus</i>		11	8	1		8	11	1	1	6	6	5	1
Total	6	32	9	1	4	31	12	1	5	16	12	9	1

¹Data from Bertelsen, 1951: 106.

Color in preservation dark brown to black over entire external surface of body except for bulb and appendages of esca (esca appendages and unpigmented distal portion of esca bulb silvery-white in unpreserved specimens of *L. acanthognathus*; E. Bertelsen, personal communication); oral cavity and guts except for outer surface of stomach wall unpigmented.

D. 5–8, first ray of dorsal fin reduced to a small stub; A. 4–7; P. 17–21 (Table 1); pelvics absent; C. 9 (2 unbranched – 4 branched – 3 unbranched); branchiostegal rays 6 (2 + 4).

Relationships. *Lophodolos* appears to be the most derived genus of the thirteen oneirodid genera. It is extremely specialized in many ways and, although probably derived from a *Microlophichthys*-like ancestor (a relatively primitive member of the family), it shows little resemblance to any other oneirodid (see Pietsch, 1974).

Distribution. Both species of *Lophodolos* have a wide horizontal distribution, and occur in all three major oceans of the world. *Lophodolos indicus* has not been taken in the western Atlantic where 82 percent of the material of *L. acanthognathus* has been collected. On the other hand, *L. acanthognathus* is represented in the eastern Pacific by only three specimens (Fig. 9).

Since virtually all collections of *Lophodolos* were made with nonclosing nets, vertical distributions are based on the maximum depths reached by fishing gear for each capture. Metamorphosed specimens were taken between approximately 650 m and an unknown lower limit. All specimens larger than 30 mm (37 individuals) were captured by nets fished below 1000 m; 62 percent of these were captured by nets fished below 1500 m. Material of both species from any one geographical area was insufficient to show whether there is any vertical separation between the two forms.

Comments. The original spelling of the generic name *Lophodolos* (Lloyd, 1909a), is reestablished as the “correct original spelling,” as provided by Article 32(a) of the International Code of Zoological Nomenclature.

Key to the Females of the Species of the Genus LOPHODOLOS

- 1A. Length of illicium less than 25 percent of SL in specimens 30 mm and larger (Fig. 1); width of esca bulb 4.4–6.7 percent of SL in specimens 25 mm and larger (Fig. 2); length of esca appendages 10.2–20.9 percent of SL in specimens 25 mm and larger, 8.7–22.2 (usually greater than 10.0) percent of SL in specimens less than 25 mm (Figs. 3–4); length of sphenotic spine 4.1–9.2 (usually greater than 6.0) percent of SL in specimens 30 mm and larger (Fig. 5); length of quadrate spine 2.9–6.5

(usually greater than 3.5) percent of SL in specimens 30 mm and larger (Fig. 6); D. 5-7 (Table 1) *L. acanthognathus* Regan, 1925.

- 1B. Length of illicium greater than 25 percent of SL in specimens 30 mm and larger (Fig. 1); width of escal bulb 2.1-4.0 percent of SL in specimens 25 mm and larger (Fig. 2); length of escal appendages 1.2-5.0 percent of SL in specimens 25 mm and larger, 4.2-10.5 (usually less than 9.0) percent of SL in specimens less than 25 mm (Figs. 3-4); length of sphenotic spine 1.9-6.0 (usually less than 5.0) percent of SL in specimens 30 mm and larger (Fig. 5); length of quadrate spine 1.6-5.0 (usually less than 3.0) percent of SL in specimens 30 mm and larger (Fig. 6); D. 6-8 (Table 1) *L. indicus* Lloyd, 1909a.

Lophodolos acanthognathus Regan, 1925

Figure 3

Oneirodes n. sp. Murray and Hjort, 1912: 104, fig. 90 (erroneous designation; specimen referred to *L. acanthognathus* by Nybelin, 1948).

Lophodolus acanthognathus Regan, 1925: 563 (original description; two specimens; lectotype designated by Bertelsen, 1951, ZMUC P92104, 12.0 mm; DANA Station 1358 (5), western North Atlantic, 28°15'N, 56°00'W; 3000 m wire; 1530 hr; 2 June 1922). Regan, 1926: 30, pl. 6, fig. 1 (brief description; one additional specimen). Regan and Trewavas, 1932: 83 (description after Regan, 1926; five additional specimens; *L. lyra* Beebe, 1932, a synonym of *L. acanthognathus*). Gregory, 1933: 402, 404, figs. 274, 276A, 277 (osteological comments; specific name misspelled *acanthagnathus* in fig. 277). Beebe, 1937: 207 (45 specimens listed from Bermuda). Nybelin, 1948: 86-89, Text-fig. 9, table 20 (*Oneirodes* n. sp. of Murray and Hjort, 1912, referred to *L. acanthognathus*; description of an additional specimen; comparison with previous descriptions; geographic, bathymetric distribution). Bertelsen, 1951: 107, figs. 64-65, tables 21-22 (synonymy; description; comparison with all known material; DANA material listed; comments; in key). Grey, 1955: 299 (one additional specimen). Grey, 1956: 255 (synonymy; vertical distribution).

Lophodolus lyra Beebe, 1932: 96-98, fig. 28 (original description; about 40 specimens; holotype, USNM 170949, 47.0 mm; GLADISFEN Net 111, 32°12'N, 64°36'W; 1463 m; 27 July 1931). Koefoed, 1944: 7, pl. 3, fig. 3 (misidentifications; description; three specimens including *Oneirodes* n. sp. of Murray and Hjort, 1912).

Lophodolos acanthognathus, Fowler, 1936: 1340, 1365, fig. 560 (corrected spelling; brief description after Regan, 1926). Pietsch, 1972a: 35, 45 (osteological comments). Pietsch, 1974: in press (osteology; relationships).

Material. Seventy-six female specimens, 6.0-70.0 mm: BMNH 4(18.0-26.0 mm); BOC 3; BZM 3(8.5-51.0 mm); FMNH 1(9.5 mm); GNM 1(56.0 mm); ISH 6(46.0-70.0

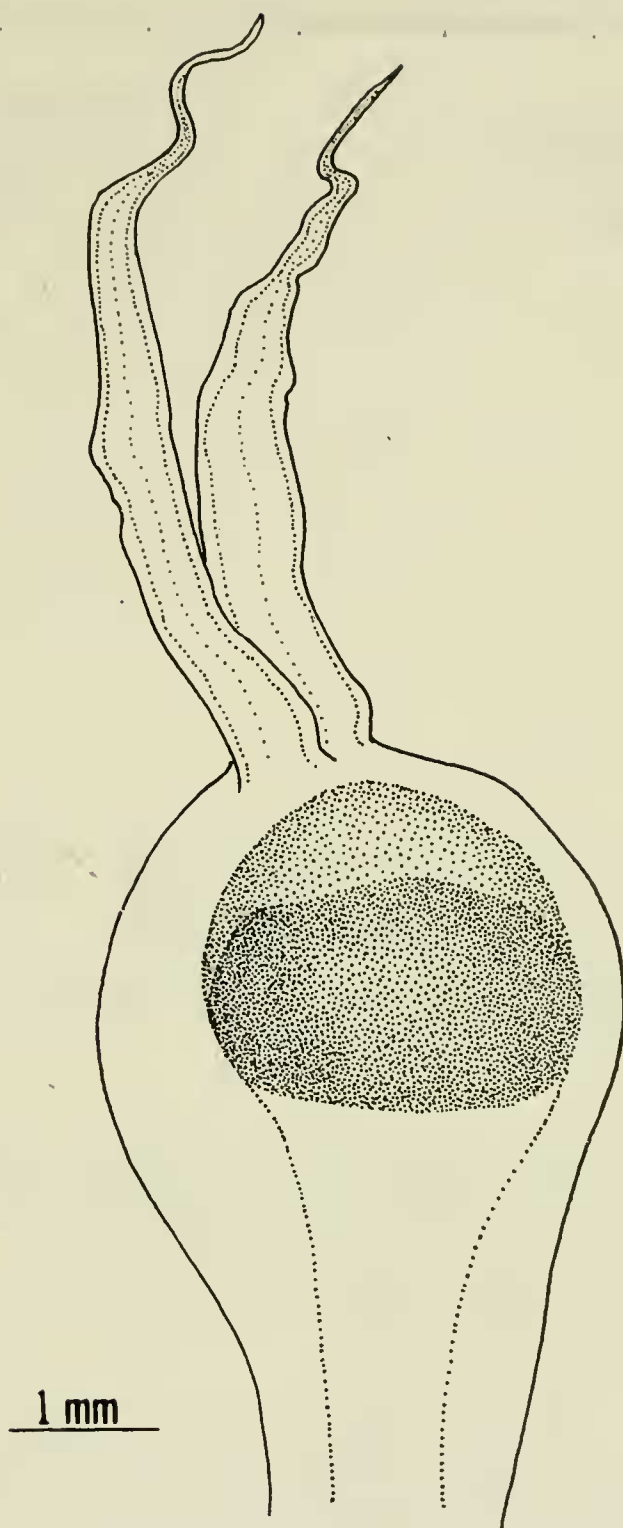


Figure 3. Esca of *Lophodolos acanthognathus*, LACM 10011-9, 38.0 mm, left lateral view. Drawn by Patricia Chaudhuri.

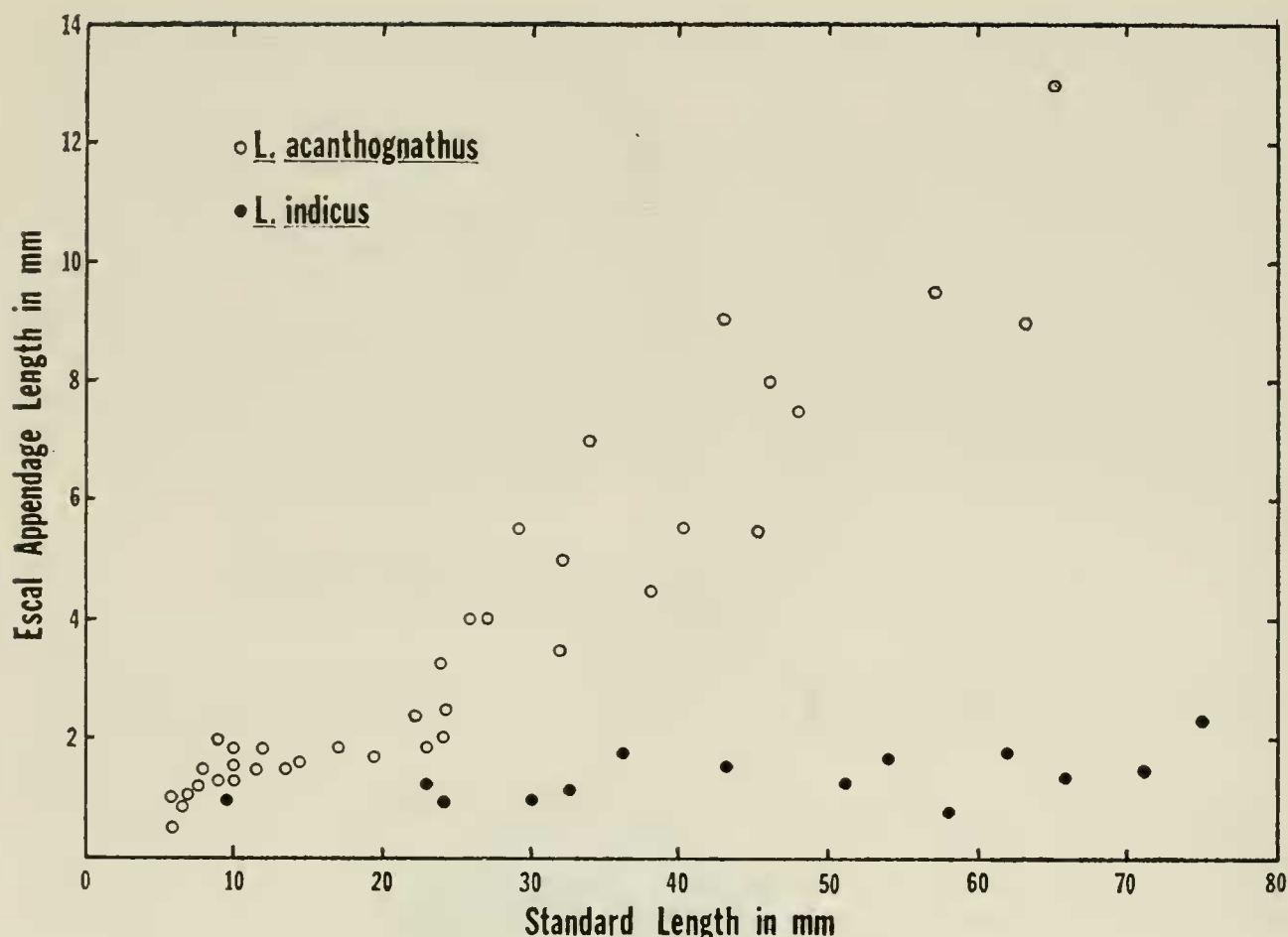


Figure 4. Relationship of escal appendage length and standard length for species of *Lophodolos*.

mm); LACM 4(22.5–38.0 mm); MCZ 2(18.0–65.0 mm); ROM 13(17.0–57.0 mm); SU 32(6.0–32.0 mm); USNM 2(10.0–47.0 mm); ZMUC 5(8.5–40.0 mm).

Diagnosis. See key to species.

Description. Illicium short, 11.1–23.1 (Fig. 1); width of escal bulb large, 4.2–9.0 (Fig. 2); escal appendages long, 8.7–22.2 (Figs. 3–4); sphenotic spines long, 4.1–9.2 (Fig. 5); quadrate spines long, 2.9–6.5 (Fig. 6); D. 5–7 (only one specimen had D. 7, ISH 500/73); A. 4–6; P. 17–21 (Table 1) (measurements in percent of SL; spine lengths based on specimens greater than 30 mm, fin ray counts on specimens greater than 20 mm).

Rest of characters as for genus.

Distribution. *Lophodolos acanthognathus* is known from both sides of the Atlantic. The vast majority of specimens (82 percent, including all type material) have been collected from the western half of this ocean as far east as 26°W, between 58°N and 25°N. In the eastern Atlantic the range extends from approximately 48°N, 18°W, southward, off the southern tip of

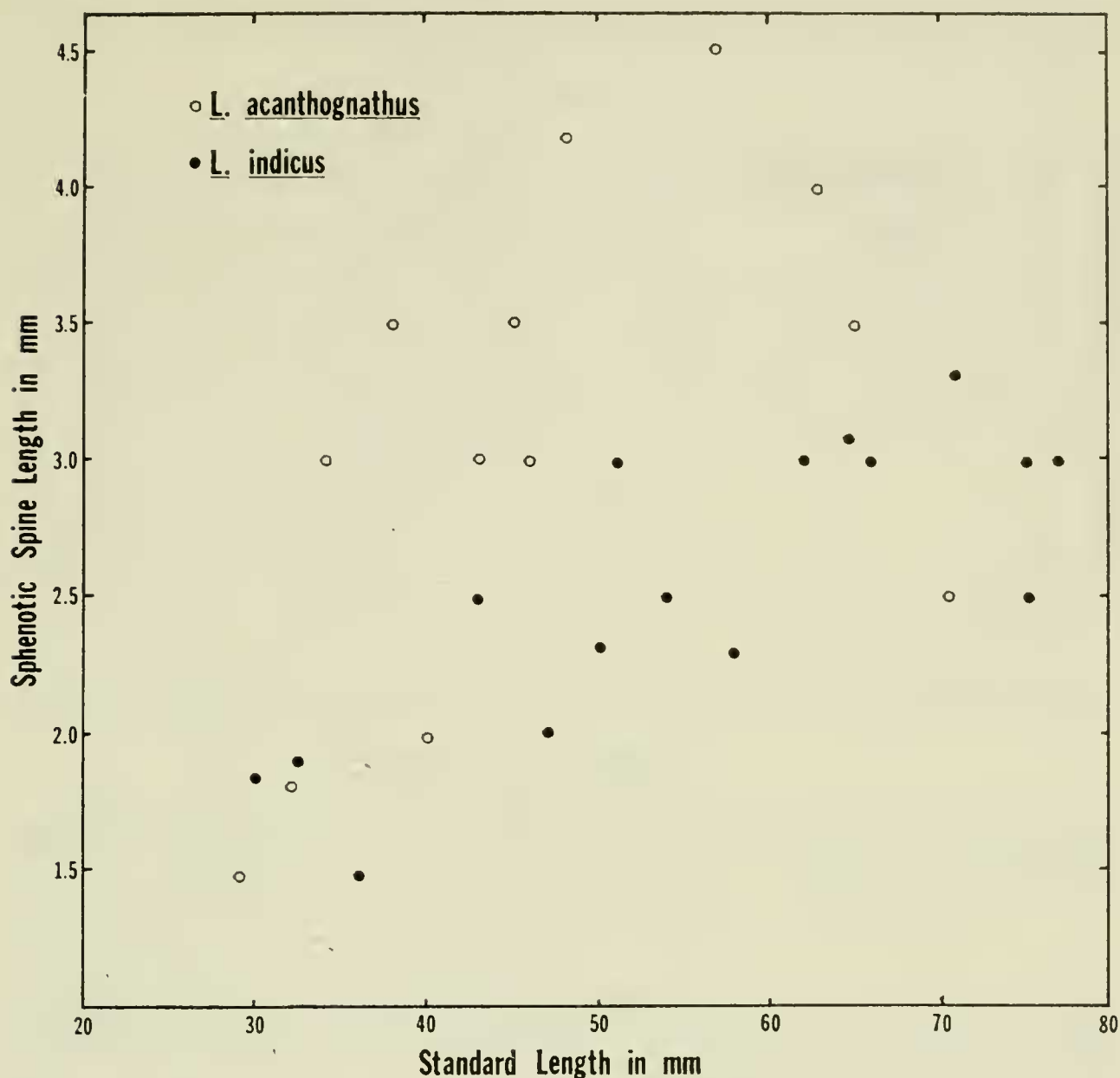


Figure 5. Relationship of sphenotic spine length and standard length for species of *Lophodolos*.

Portugal and the continental slope of Africa to 2°S , 26°W . A single record is known from the central South Atlantic at approximately 40°S , 26°W .

In the Indo-Pacific region *L. acanthognathus* is represented by three specimens: one from the Bay of Bengal, Indian Ocean (at approximately 7°N , 60°E), and two from the South China and Celebes seas. Three records are known from eastern Pacific Equatorial waters: on the equator at 139°W and from off the coast of Peru. The lectotype was collected from the western north Atlantic at $28^{\circ}15'\text{N}$, $56^{\circ}00'\text{W}$ (Fig. 9).

On the basis of maximum depths reached by fishing gear, metamorphosed *L. acanthognathus* are vertically distributed between approximately 650 m and an unknown lower limit. All

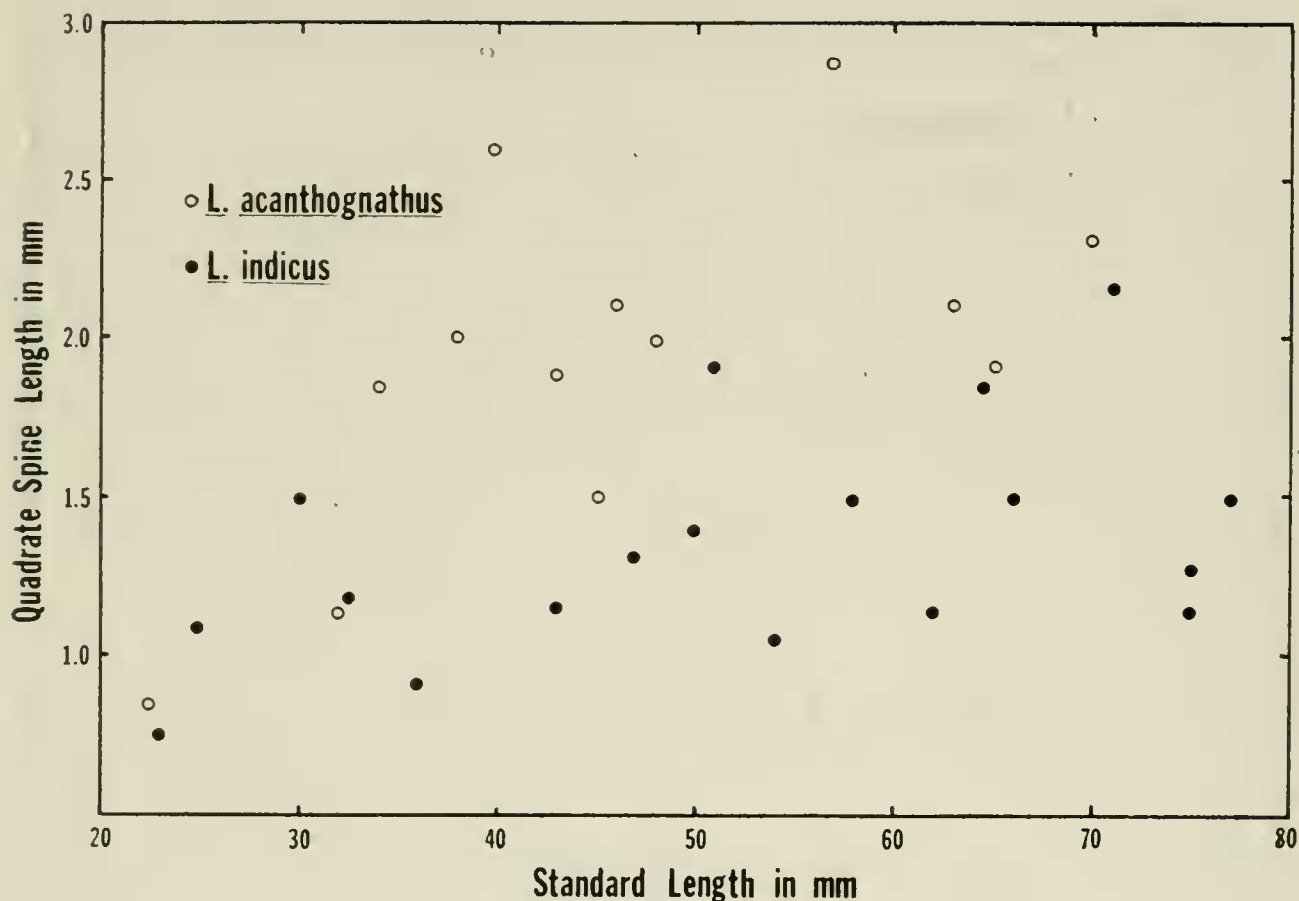


Figure 6. Relationship of quadrate spine length and standard length for species of *Lophodolos*.

specimens larger than 30 mm (19 individuals) were captured by nets fished below 1000 m; 58 percent of these were captured by nets fished below 1500 m.

Comments. Specimens of *L. acanthognathus* larger than approximately 30 mm can easily be separated from *L. indicus* on the basis of illicial and escal appendage lengths alone (see key to species). Smaller specimens, especially those less than 20 mm, are difficult to identify, and require a combination of meristics and counts, all of which overlap between the two species: illicial and escal appendage lengths, width of escal bulb, and dorsal fin ray counts (See Figs. 1–2, 4, Table 1). In some cases, geographic distribution may provide additional data for identification; *L. indicus* apparently does not occur in the western North Atlantic where approximately 82 percent (62 individuals) of the known material of *L. acanthognathus* has been collected (Fig. 9).

The holotype *L. lyra* Beebe (1932) compares well with the known material of *L. acanthognathus*; the name is retained as a synonym of *L. acanthognathus* following Regan and Trewavas (1932).

Lophodolos indicus Lloyd, 1909a

Figures 7–8

Lophodolos indicus Lloyd, 1909a: 167 (original description; single specimen; holotype, IMC 1024/1, 53.0 mm; INVESTIGATOR Station 307, off Kerala (formerly Travancore), southwest coast of India: 0–1624 m).

Lophodolus indicus, Lloyd, 1909a: pl. 45, fig. 7 (holotype figured). Regan, 1925: 563 (comparison with *L. acanthognathus*). Regan, 1926: 30 (brief description after Lloyd, 1909a; comparison with *L. acanthognathus*). Regan and Trewavas, 1932: 83 (after Lloyd, 1909a, Regan, 1926). Bertelsen, 1951: 108 (description after Lloyd, 1909a, Regan and Trewavas, 1932; comparison with all known material of *Lophodolos*). Grey, 1956: 255–256 (synonymy; vertical distribution).

Lophodolus dinema Regan and Trewavas, 1932: 83, pl. 4, fig. 3 (original description; single specimen; holotype, ZMUC P92105, 43.0 mm; DANA Station 3716 (2), South China Sea, 19°18'N, 120°13'E; 3000 m wire; bottom depth 3225 m; 1400 hr; 22 May 1929). Bertelsen, 1951: 108 (description; comparison with all known material of *Lophodolos*). Grey, 1956: 255 (synonymy; vertical distribution).

Material. Twenty-two female specimens, 9.5–77.0 mm: IMC 1 (53.0 mm); ISH 5 (36.0–75.0 mm); LACM 4 (32.5–71.0 mm); MCZ 4 (30.0–64.5 mm); NIO 1 (57.0 mm); SIO 5 (9.5–77.0 mm); UMML 1 (23.0 mm); ZMUC 1 (43.0 mm).

Diagnosis. See key to species.

Description. Illicium long, 15.2–138.0 (Fig. 1); width of escal bulb small, 2.1–5.2 (Fig. 2); escal appendages short, 1.2–10.5 (Figs. 4, 8); sphenotic spines short, 1.9–6.0 (Fig. 5); quadrate spines short, 1.6–5.0 (Fig. 6); D. 6–8; A. 5–7; P. 17–21 (Table 1) (measurements in percent of SL; spine lengths based on specimens greater than 30 mm, fin ray counts on specimens greater than 20 mm).

Rest of characters as for genus.

Distribution. In the Atlantic Ocean, *L. indicus* appears to be restricted to the eastern side; seven specimens are known from off the continental slope of Africa from 20°N, 21°W, east to the Gulf of Guinea and south to approximately 18°S, 10°W. The remaining material (15 specimens) is rather evenly distributed across the Indian and Pacific oceans between approximately 4°S and 30°N. The holotype was collected off the southwest coast of India (Fig. 9).

On the basis of maximum depths reached by fishing gear, metamorphosed *L. indicus* are vertically distributed between approximately 750 m and an unknown lower limit. All specimens larger than 30 mm (18 individuals) were captured by

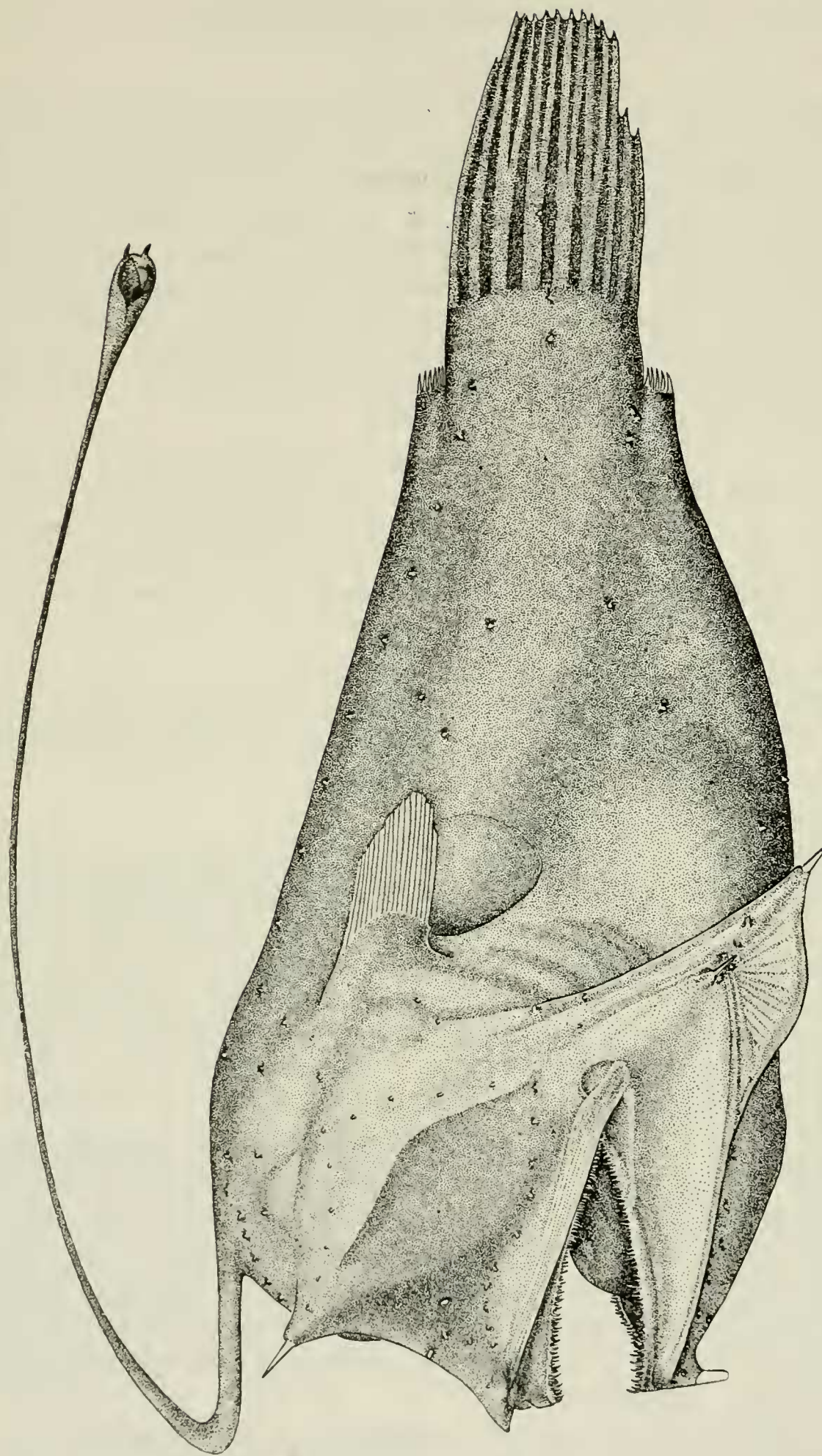


Figure 7. *Lophodolos indicus*, MCZ 47559, 58.0 mm. Drawn by Patricia Chaudhuri.

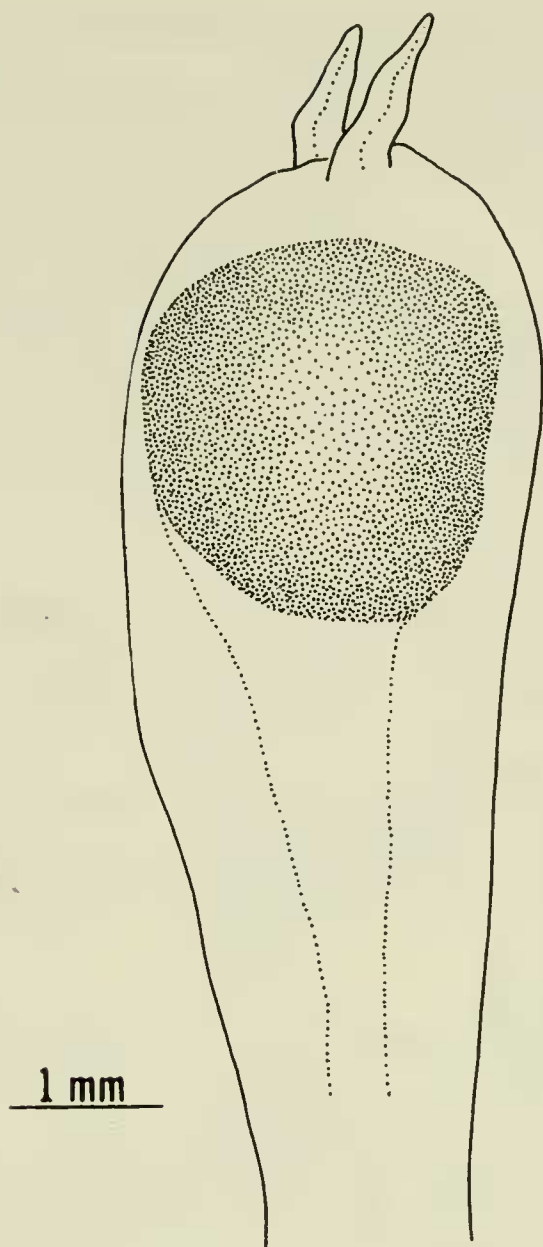


Figure 8. Esca of *Lophodolus indicus*, MCZ 47559, 58.0 mm, left lateral view. Drawn by Patricia Chaudhuri.

nets fished below 1000 m; 67 percent of these were captured by nets fished below 1500 m.

Comments. Large specimens of *L. indicus* (greater than approximately 30 mm) are easily distinguished from *L. acanthognathus* on the basis of illicial and esca appendage lengths alone (see key to species). Smaller specimens are more difficult to identify (see comments under *L. acanthognathus*).

Lophodolus dinema Regan and Trewavas (1932) was described as new on the basis of an esca morphology differing from that of *L. indicus*. These differences, however, are undoubtedly the result of damage. The esca of the holotype of *L. indicus*, originally described by Lloyd (1909a: 167) as being "hard but . . . covered with short, shreddy filaments," has lost

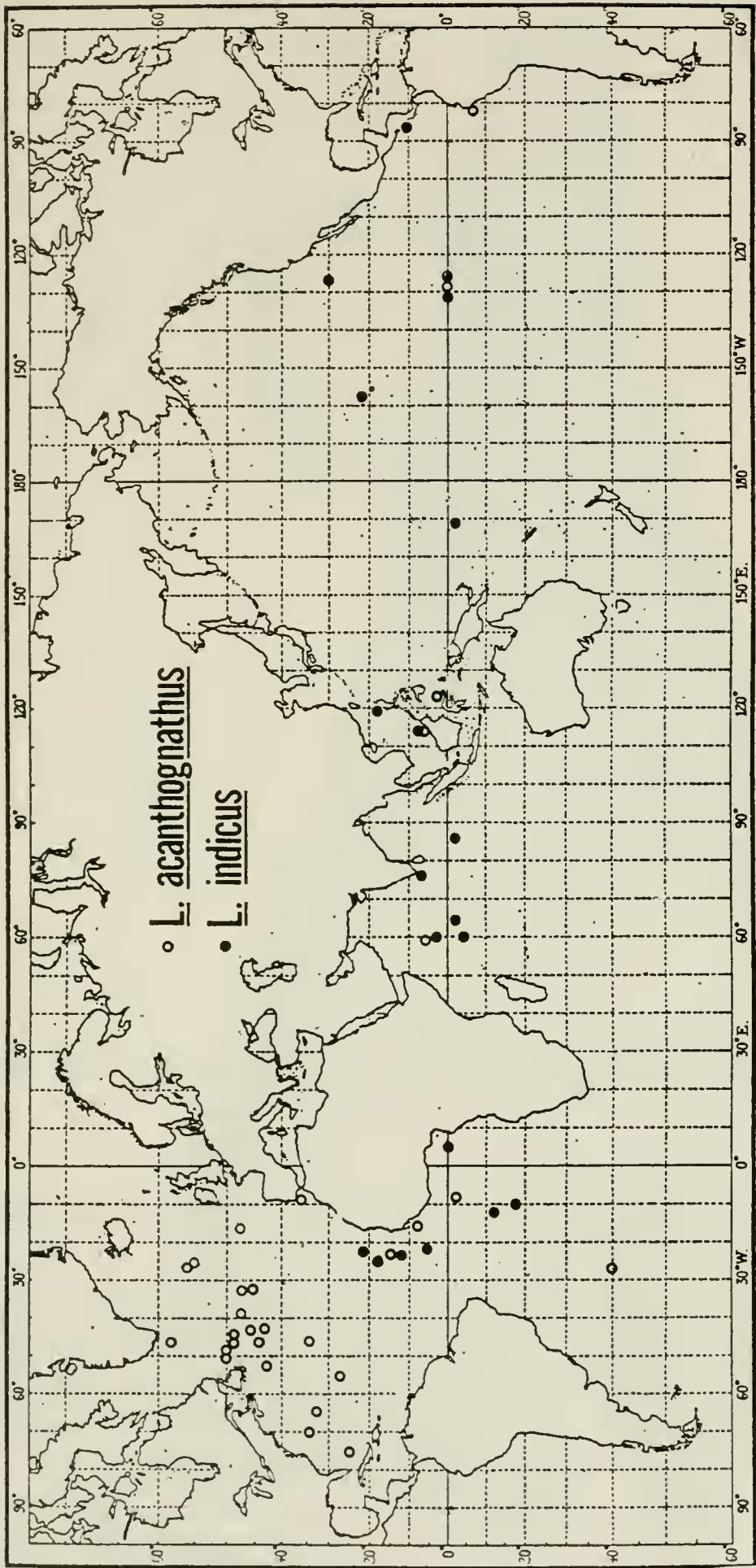


Figure 9. Known geographical distribution of species of *Lophodolos*. A single symbol may represent more than one capture.

the two bilaterally placed appendages found in the holotype of *L. dinema* and in all known specimens of *Lophodolos*. Although I did not see it, the poor condition of the esca was confirmed by a sketch made from the holotype of *L. indicus* provided by A. G. K. Menon of the Zoological Survey of India. Discrepancies in illicial length (Bertelsen, 1951: 107) are also more apparent than real. A plot of illicial length against standard length (Fig. 1) shows the holotype of *L. dinema* to compare well with the material here considered to be *L. indicus*. In the absence of any significant differences, *L. dinema* is here synonymized with *L. indicus*.

SPECIES INCERTAE SEDIS

Lophodolos biflagellatus Koefoed, 1944, *nomen nudum*.

Lophodolus biflagellatus Koefoed, 1944: 7.

Comments. This name was used by Koefoed in a manuscript dated 1918 (not seen by me), and later mentioned in published form (Koefoed, 1944: 7) without application to a description or type.

SPECIES RELATIONSHIPS

Lophodolos acanthognathus and *L. indicus* are distinguished on the basis of five characters: illicial length, esca bulb width, esca appendage length, sphenotic spine length, and quadrate spine length. For most of these characters it is difficult, if not impossible, to know whether a character state represents a primitive or a derived condition. The longer illicium of *L. indicus* (Fig. 1), however, is surely a derived state; an increase in illicial length is a trend found within other oneirodid genera (*Dolopichthys*, *Oneirodes*, and *Chaenophryne*; Pietsch, 1972b, 1974). The width of the esca bulb of *L. acanthognathus* is like that of nearly all other oneirodids; the considerably narrower bulb of *L. indicus* (Fig. 2) is most likely a derived condition. *Lophodolos acanthognathus* has significantly longer esca appendages than *L. indicus* (Fig. 4), perhaps representing a derived state; longer esca appendages and filaments are found in the more derived species of *Oneirodes* (Pietsch, 1974). The sphenotic and quadrate spines of *L. acanthognathus* are long relative to those of *L. indicus*; either character state, long versus short, may represent the derived condition. From this character analysis, it is reasonable to speculate that *L. indicus* is the more derived member of the genus.

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